

Some Effects of Low-intensity Fires on Populations of Co-occurring Small Trees in the Sydney Region

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Nine species of small tree were studied one year after low-intensity prescribed fires in 1991 and 1992 at a site in the outer western region of the Sydney metropolitan area. All of the species except *Hakea sericea* proved to be fire-tolerant, with less than one-third of the plants killed by the fires. All of the fire-tolerant species had smaller stems killed by the fires, the size of surviving stems being related to their fire-tolerance characteristics for most of the species — *Leptospermum trinervium* and *Persoonia linearis* (with dormant epicormic and lignotuber buds) survived at relatively small stem sizes, with *Casuarina torulosa* and *Jacksonia scoparia* (with dormant buds at the stem base) surviving at larger sizes, and *Acacia binervia* and *Casuarina littoralis* (with no dormant buds) surviving only at the largest stem size. Both *Acacia implexa* (with root suckers) and *Acacia parramattensis* (with no dormant buds) were exceptions to this generalization.

The size structure of the stem populations was significantly different in the burnt areas compared to an adjacent unburnt area for all six species for which there were data. All four of the species that are capable of producing new post-fire shoots at the stem base preferentially did so when the upper stem had been killed, and the number of shoots produced was usually unrelated to the size of the stem. Both of the species that are capable of producing new post-fire epicormic shoots almost invariably did so if the stem was alive post-fire, and for both species the number of shoots produced was related to the size of the stem.

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INTRODUCTION

Knowledge of the responses of plant species to fires is of intrinsic interest as well as being essential for the scientific management of plant communities (Gill and Bradstock, 1992). For example, two general types of regeneration strategy by plant populations after fire are usually recognized:— death of all adult plants during the fire followed by regeneration solely from seeds (fire-sensitive species); and regeneration from protected dormant vegetative buds on adult plants that survive the fire (fire-tolerant species) (Gill, 1981). These two strategies result in dramatically different population dynamics, and vegetation management for species conservation may need to incorporate these differences into fire-management plans (Bradstock and Auld, 1987).

There is an increasing amount of quantitative data on the post-fire behaviour of both fire-sensitive species (e.g. Bradstock and Myerscough, 1981; Auld, 1987; Bradstock and O'Connell, 1988; Lamont *et al.*, 1991) and fire-tolerant species (e.g. Gill and Ingwersen, 1976; Lamont and Downes, 1979; Auld, 1986; Zammit and Westoby, 1987; Bradstock and Myerscough, 1988; Bradstock, 1990; Davies and Myerscough, 1991; Lamont and Runciman, 1993) in Australia. However, there have been few comparative studies of co-occurring species (e.g. Beadle, 1940; Hodgkinson and Griffin, 1982; Benson, 1985; Delfs *et al.*, 1987; Clark, 1988; Cowling *et al.*, 1990; Auld and O'Connell, 1991).

The work reported here seeks to compare some of the population responses to low intensity prescribed fires of a range of co-occurring species of small tree from the Sydney region. In particular, the following questions were addressed:—

- 1) which of the species are fire-tolerant as adult plants, and what characteristics allow them to be so?
- 2) for those species with some degree of fire-tolerance, what is the minimum stem size necessary for post-fire survival?
- 3) for these same species, how does the post-fire death of plants affect the size/age structure of the population?
- 4) for those species that can regenerate post-fire shoots from dormant buds, what is the pattern of post-fire shoot production from these epicormic and/or stem basal buds?

MATERIALS AND METHODS

The work was carried out on the 'Yarrowood' property of the University of Technology, Sydney, at Yarramundi in the outer western region of the Sydney metropolitan area. The vegetation is an open-forest dominated by *Eucalyptus punctata*, *E. fibrosa*, *E. eximia* and *E. oblonga* (vegetation type 10ar[iii] of Benson, 1992), occurring on both sandstone and shale substrates. The vegetation is thus not uniform throughout the area, but varies with soil type (sand versus clay) and aspect (Benson, 1992). Most of the small tree species are disjunctly distributed on the property, depending on their habitat preferences.

The majority of the vegetation has been subjected to prescribed fires since the late 1960s, although the western end of the property was last burnt by a high-intensity wildfire in 1968. About half of the property was burnt by a low-intensity prescribed fire in the autumn of 1991 and most of the rest was burnt by a low-intensity prescribed fire in the autumn of 1992. Both fires varied spatially in intensity, with scorch height varying from 2–4 m. Study samples were taken from these two areas 1 year after each of these fires and also from the unburnt western area in April of 1992 and 1993. All of the samples from the two burnt areas were combined for data analysis.

Plants were sampled by locating as many individuals of the small tree species as possible in each of the three study areas. Small tree species were defined as those species with adult plants with stems usually above 2 m tall on the 'Yarrowood' property. For each individual plant the following characteristics were recorded:—whether the stem was dead or alive (i.e. whether it had clear evidence of green shoots, either surviving pre-fire shoots or new post-fire shoots); stem circumference at 1 m height; number of post-fire aerial (epicormic) shoots; number of post-fire shoots at the stem base (either from a lignotuber or from the bottom 30 cm of the trunk, depending on the species). Individual plants were measured only if their stem was greater than 1 m tall or they had clear evidence of post-fire shoot regeneration. This sampling programme assumed that stem death was always a response to the most recent fire (in the burnt areas), that no plant with a stem greater than 1 m tall was completely consumed by the most recent fire, and that stem growth since the fire was randomized across all samples and produced variability that was no larger than the variability due to measurement precision.

The stem circumferences of plants in the different sample areas were compared using log-likelihood ratio contingency tests on the frequency histograms for each species (Wilkinson, 1989). The median stem circumference necessary for post-fire survival (i.e. the stem size at which there is a probability of 0.5 of the stem surviving the fire) was estimated using the trimmed Spearman-Kärber method for each species (Hamilton *et al.*, 1977). The number of shoots produced by plants with live and dead stems were compared using log-likelihood ratio contingency tests on the frequency histograms for each species (Wilkinson, 1989). The relationships between stem circumference and the number of post-fire shoots for each species were assessed using Spearman rank-order correlation coefficients (Minitab Inc., 1991).

Adult plant density was also recorded in the area burnt by the prescribed fires (one

or both fires, depending on the species) and in the unburnt area. The number of individual live plants greater than 2m tall of each small tree species was recorded in each of six replicate 15m x 15m quadrats in each of these two areas. Plant abundance was compared between the two areas using Kruskal-Wallis tests for each species (Minitab Inc., 1991).

RESULTS

Nine species of small tree were common enough on the 'Yarrowood' property to be studied (Table 1). Other small tree species recorded, for which less than 50 individuals were located, include:— *Acacia longifolia* Andrews (Willd.), *Acacia trinervata* Sieber ex DC., *Banksia serrata* L.f., *Exocarpos cupressiformis* Labill., *Persoonia levis* (Cav.) Domin, and *Xylomelum pyriforme* (Gaertner) Knight.

Of these nine species, only *H. sericea* had a significantly different abundance of adults between the burnt and unburnt areas (Table 2), suggesting that all of the other species have some degree of tolerance to low-intensity fires as adults. For the other species, up to one-third of all of the plants located post-fire had been killed by the fires (Table 2); death of the plants could not be determined for the two species with root suckers (*A. implexa* and *J. scoparia*).

TABLE 1
Species of single-stemmed small tree studied, and their fire-regeneration characteristics

Species	Family	Maximum height (m)	Stem aerial buds	Stem basal buds	Root buds
<i>Acacia binervia</i> (H. L. Wendl.) J. F Macbr.	Mimosaceae	10	—	—	—
<i>Acacia implexa</i> Benth.	Mimosaceae	6	—	—	suckers
<i>Acacia parramattensis</i> Tind.	Mimosaceae	7	—	—	—
<i>Casuarina littoralis</i> Salisb.	Casuarinaceae	8	—	—	—
<i>Casuarina torulosa</i> Aiton	Casuarinaceae	8	—	stem base	—
<i>Hakea sericea</i> Schrader	Proteaceae	3	—	—	—
<i>Jacksonia scoparia</i> R. Br.	Fabaceae	3	—	stem base	suckers
<i>Leptospermum trinervium</i> (Smith) J. Thompson	Myrtaceae	4	epicormic	lignotuber	—
<i>Persoonia linearis</i> Andrews	Proteaceae	4	epicormic	lignotuber	—

All of the eight species with adult fire-tolerance had relatively smaller stems killed by the fires (Fig. 1, Table 3) and the minimum stem size necessary for post-fire survival varied widely between these species (Table 4). Furthermore, the size structure of the stem populations was significantly different in the area subject to prescribed fires compared to the unburnt area for all six species for which there were data (Fig. 1, Table 3).

All four of the species that are capable of producing new post-fire shoots at the stem base preferentially did so when the upper stem had been killed (Fig. 2, Table 3), and the number of shoots produced was usually unrelated to the size of the stem (only for *C. torulosa* was the relationship between stem circumference and number of basal shoots statistically significant) (Fig. 3). Both of the species that are capable of producing new post-fire epicormic shoots almost invariably did so if the stem was alive post-fire (Fig. 4), and for both species the number of shoots produced was statistically significantly related to the size of the stem (Fig. 5).

TABLE 2

Density of live adult plants of the small tree species in the area subject to the prescribed fires in either 1991 or 1992 and in the unburnt area, and the number of plants apparently killed by the fires.

Species	Density (plants/225m ²)*		Kruskal-Wallis test		% of plants killed by the low-intensity fires (n)
	Unburnt area	Burnt area	H	P	
<i>Acacia binervia</i>	0.00 (0.00)	2.50 (2.50)	1.00	0.318	25.9 (212)
<i>Acacia implexa</i>	0.00 (0.00)	4.00 (4.00)	1.00	0.318	- +
<i>Acacia parramattensis</i>	3.83 (2.46)	2.33 (1.50)	0.15	0.703	17.4 (138)
<i>Casuarina littoralis</i>	1.17 (0.75)	3.83 (2.59)	0.15	0.703	33.6 (321)
<i>Casuarina torulosa</i>	9.00 (5.59)	11.67 (3.52)	1.09	0.297	8.2 (170)
<i>Hakea sericea</i>	30.33 (7.49)	0.00 (0.00)	9.47	0.002	100.0 (56)
<i>Jacksonia scoparia</i>	6.17 (2.68)	1.67 (1.28)	2.94	0.087	- +
<i>Leptospermum trinervium</i>	24.00 (6.83)	10.83 (4.85)	1.89	0.169	5.0 (261)
<i>Persoonia linearis</i>	10.17 (2.46)	4.83 (2.06)	2.58	0.108	0.0 (153)

* Mean (standard error).

+ Species has suckers, and so death of a plant was not determinable.

TABLE 3

Results of the log-likelihood ratio contingency tests for the comparison of the frequency histograms of stem circumference and number of basal shoots for the small tree species.

Species	Stem circumference of alive versus dead stems in the burnt area		Stem circumference of alive stems in the burnt versus unburnt areas		Number of post-fire basal shoots of alive versus dead stems	
	G	P	G	P	G	P
<i>Acacia binervia</i> *	117.01	<0.001	—	—	—	—
<i>Acacia implexa</i> *	46.27	<0.001	—	—	—	—
<i>Acacia parramattensis</i>	49.62	<0.001	15.92	0.007	—	—
<i>Casuarina littoralis</i>	179.84	<0.001	46.62	<0.001	105.18	<0.001
<i>Casuarina torulosa</i>	121.25	<0.001	26.15	<0.001	—	—
<i>Hakea sericea</i> +	—	—	—	—	—	—
<i>Jacksonia scoparia</i>	43.38	<0.001	53.52	<0.001	50.18	<0.001
<i>Leptospermum trinervium</i>	129.21	<0.001	17.78	0.001	52.33	<0.001
<i>Persoonia linearis</i>	70.64	<0.001	19.36	0.001	121.77	<0.001

* No stems were found in the unburnt area.

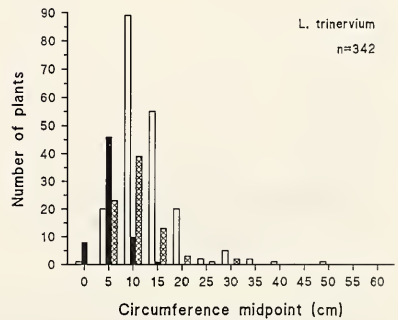
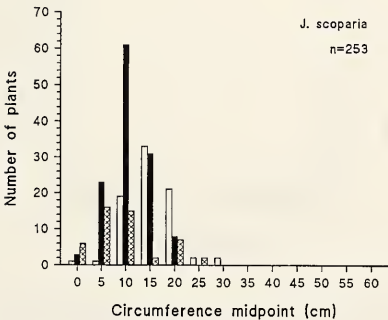
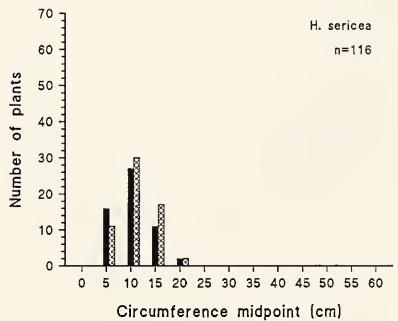
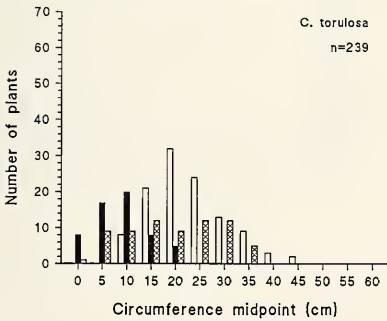
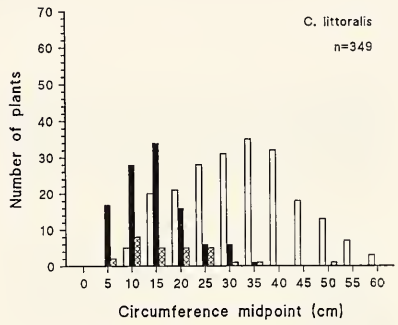
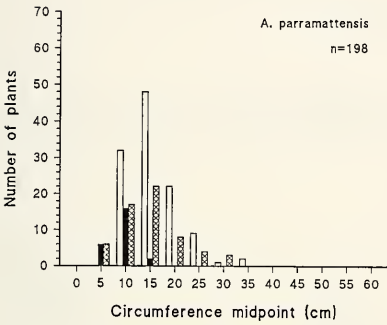
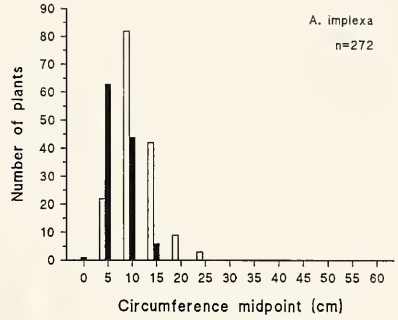
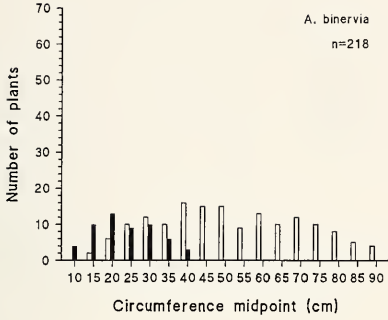
+ No live stems were found in the burnt area.

TABLE 4

Median stem size that the species of small tree must reach before the stem is capable of surviving a low-intensity fire

Species	Stem circumference (cm)*	
<i>Acacia binervia</i>	(22.2)	24.9 (28.0)
<i>Acacia implexa</i>	(6.9)	7.7 (8.5)
<i>Acacia parramattensis</i>	(8.0)	8.6 (9.3)
<i>Casuarina littoralis</i>	(15.2)	16.7 (18.5)
<i>Casuarina torulosa</i>	(10.6)	11.9 (13.4)
<i>Jacksonia scoparia</i>	(12.5)	13.7 (15.0)
<i>Hakea sericea</i>		
<i>Leptospermum trinervium</i>	(5.7)	6.3 (6.9)
<i>Persoonia linearis</i>	(5.7)	6.4 (7.2)

* median (95% confidence limits).



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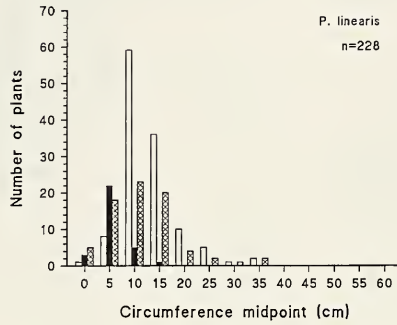


Fig 1. Frequency histograms of stem circumference at 1m height for nine single-stemmed small tree species. Alive stems in the burnt areas (open bars); dead stems in the burnt areas (filled bars); alive stems in the unburnt area (hatched bars); n: number of stems sampled.

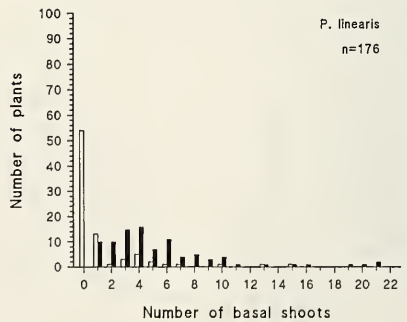
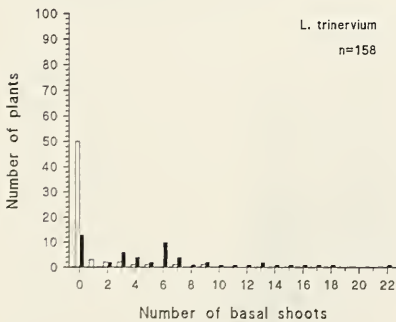
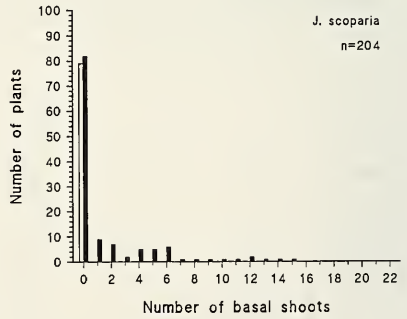
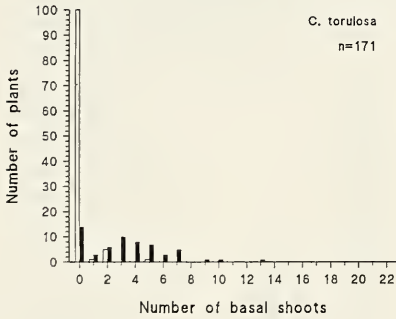


Fig. 2. Frequency histograms of the number of post-fire basal (lignotuber or base of stem) shoots per stem for four small tree species. Alive stems (open bars); dead stems (filled bars); n: number of stems sampled.

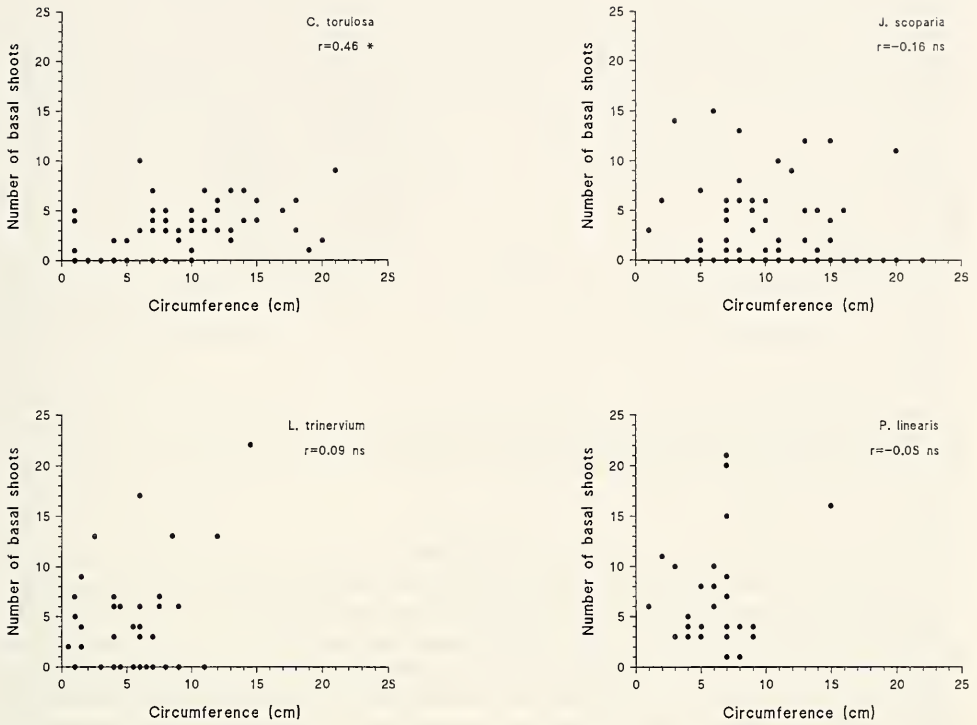


Fig. 3. Relationship between the number of post-fire basal (lignotuber or base of stem) shoots per stem and stem circumference at 1 m height for four small tree species. r: Spearman rank correlation coefficient; $P < 0.001$, ns: not significant.

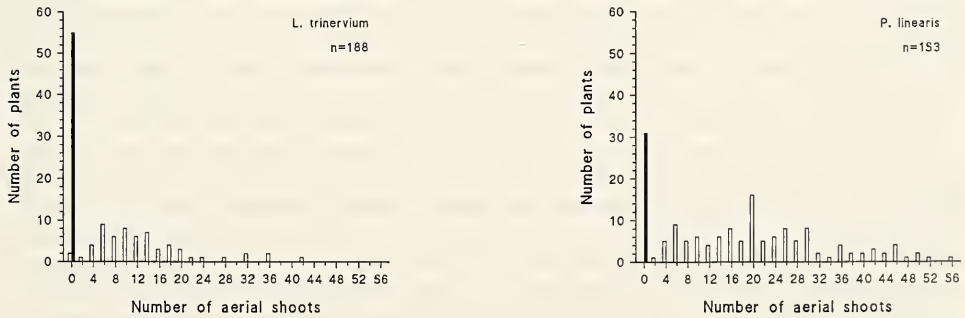


Fig. 4. Frequency histograms of the number of post-fire aerial (epicormic) shoots per stem for two small tree species. Alive stems (open bars); dead stems (filled bars); n: number of stems sampled.

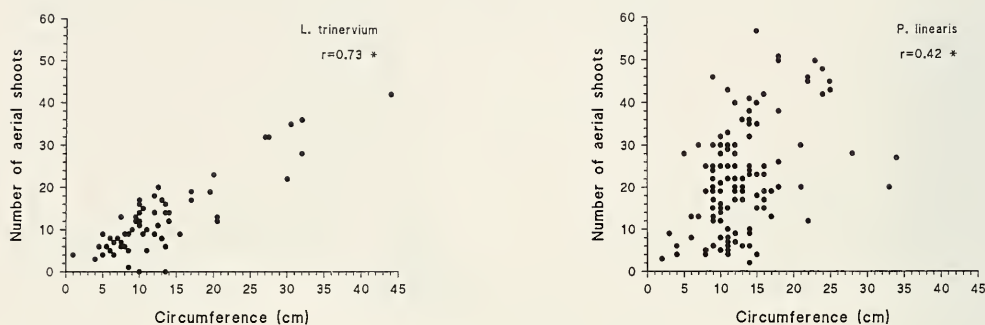


Fig. 5. Relationship between the number of post-fire aerial (epicormic) shoots per stem and stem circumference at 1m height for two small tree species. r : Spearman rank correlation coefficient; * $P < 0.001$.

DISCUSSION

The nine co-occurring species of small trees studied displayed a wide range of responses to the low-intensity fires encountered at 'Yarrowood'.

Only *H. sericea* appears to be incapable of surviving low-intensity fires as adult plants (i.e. is fire-sensitive), thus relying entirely on regeneration of new individuals from the canopy-stored seedbank for continuation of the populations. This strategy does not appear to be successful at 'Yarrowood', as no seedlings of this species were observed to become established after either of the two prescribed fires and there were no surviving adults. Local extinction of a fire-sensitive species will occur if an inter-fire interval (the time between successive fires) is shorter than the time taken for the plants to reach first reproduction (the primary juvenile period) (e.g. Bradstock and O'Connell, 1988; Pannell and Myerscough, 1993) and this may well be the case for this species at 'Yarrowood'.

Most of the species showing adult tolerance of the low-intensity fires do not show an absolute ability to survive the fires, with up to 34% of the adult plants apparently being killed by the fires. Only for *P. linearis* were no plants located without post-fire shoots, although this may simply be a sampling error since it is clearly better to label live plants before the fire and then check for post-fire death (my estimates of the number of deaths are thus minimum estimates). Death of the plants could not be determined for the two species with root suckers (*A. implexa* and *J. scoparia*), and the physiology and ecology of root-suckering in relation to fire is a neglected area of research (Ashton, 1981).

However, all of these eight species can be classified as fire-tolerant for low-intensity fires using the 'general rule' (less than one-third of plants killed by the fire) of Gill and Bradstock (1992). It is quite common for species to display variable survival rates even within the one fire (e.g. Beadle, 1940; Hodgkinson & Griffin 1982; Clark, 1988), as displayed by the small tree species, presumably as a result of variation in both fire intensity and size-related fire resistance of the plants (Hodgkinson & Griffin, 1982; Clark, 1988).

Many of the smaller stems of the individuals were killed for all of the fire-tolerant species. Individual plants must thus attain a certain minimum stem size before they are fire-tolerant (i.e. so that the temperature of the meristem tissue is not raised to lethal levels), and this size is presumably related to several growth characteristics that may

protect the living tissue of the plant from the heat of the fire (Gill, 1981). First, as secondary growth progresses bark is formed on the outer surface of the trunk, which may provide a protective insulating layer (the periderm protecting the cambium) that becomes increasingly effective as the stem ages. Secondly, as the stem height increases an increasingly larger amount of the foliage may be held above the scorch height of the flames (i.e. the plant canopy may not be subject to 100% scorch). Thirdly, there may be protected dormant vegetative buds, either on the aerial parts of the stem itself or at its base, and the degree to which these buds are protected may increase as the stem ages.

Two of the eight species (*L. trinervium* and *P. linearis*) have stems with both aerial and basal (lignotuber) protected dormant vegetative buds as well as quite specialized insulating flakey bark, and stems of these species can survive the low-intensity fires at quite small sizes (6 – 7cm circumference at 1m height); two of the species (*C. torulosa* and *J. scoparia*) have stems with only basal (non-lignotuber) protected dormant vegetative buds, and stems of these species must be larger before they can survive the low-intensity fires (11 – 14cm circumference); and two of the species (*A. binervia* and *C. littoralis*) do not have any protected dormant vegetative buds, and stems of these species must be relatively large before they can survive the low-intensity fires (16 – 25cm circumference). Thus there is an apparently logical sequence, whereby species with fewer fire-protection mechanisms require stems of larger size before they are capable of surviving fires. The two exceptions to this sequence are *A. implexa* and *A. parramattensis*, the stems of both of which appear to be able to survive fires at very small sizes (7 – 9cm circumference) without protected vegetative buds. However, both of these species grow rapidly (as do many other acacias), thus lifting the canopy above flame scorch height on stems that have quite small circumferences, and it may also be worth investigating the characteristics of the bark (e.g. thermal diffusivity, thickness, flammability; Gill, 1981) of these species.

No growth data exist for any of these species (*cf.* Pannell and Myerscough, 1993), but if they did then it would be possible to also calculate the length of time necessary for each of these species to become fire-tolerant (assuming that stem size is related to age). This time is clearly important for vegetation management purposes — if an inter-fire interval is shorter than the time required for a species to become fire-tolerant then new individuals will not be recruited to the population and local extinction will result (e.g. Bradstock and Myerscough, 1988).

It is important to note that the response of the species to high-intensity fires may be quite different to that observed for the low-intensity fires at 'Yarrawood'. The minimum fire-tolerant size of the stems for high-intensity fires would presumably be much larger for each species, as the heat influx to the stem and the scorch height will both be increased. It is likely that adult stems of the four species without protected buds (*A. binervia*, *A. implexa*, *A. parramattensis* and *C. littoralis*) may not survive high-intensity fires at all (i.e. the species are fire-sensitive) and nor may the two species with protected buds only at the stem base (*C. torulosa* and *J. scoparia*), although plants of *A. implexa* and *J. scoparia* may survive due to their root suckers. This may explain why Benson (1981) lists *A. parramattensis* and *C. littoralis* as fire-sensitive species rather than as fire-tolerant. However, Fox (1988) also considers *C. torulosa* to be fire-tolerant.

The size-structure of the populations in the burnt and unburnt areas is markedly different for all of the fire-tolerant species. If the pre-fire structure was similar at some time in the recent past then these differences must be the result of differences in the effect of the subsequent fire regimes (i.e. intensity, frequency, season) on the post-fire re-establishment of the populations in the two areas. For most of the species there are relatively more smaller stems in the unburnt area, as would be expected if it is the increased fire frequency in the burnt area that is causing the structural differences. Consequently, it may be reasonable to conclude that the local fire regime has had a significant impact on the relative abundances of these species, and will continue to do so for as long as the current fire management practices continue. If new individuals of these small tree species are not

allowed to be recruited to the populations at some time in the future then the populations will eventually become senescent. None of the largest stems were killed by either of the prescribed fires, suggesting that the populations have not yet reached this senescent stage.

All four of the species with protected buds at the stem base (*C. littoralis*, *J. scoparia*, *L. trinervium* and *P. linearis*) do not usually produce new shoots unless the upper part of the stem has been killed, irrespective of whether these shoots are from lignotuber buds or not, and the number of shoots produced is usually unrelated to the size of the stem. Therefore, these basal shoots may be viewed as a back-up mechanism that is only employed by the plants when the protection of the stem itself from the heat of the fire fails.

Both of the species with protected epicormic buds almost invariably produce post-fire shoots if the stem is still alive, irrespective of whether part of the pre-fire canopy is still alive or not, and the number of shoots produced is directly related to the size of the stem. Therefore, these aerial shoots may be viewed as part of an active post-fire regeneration strategy by the stem rather than as a passive survival of the fire (as in *A. parramattensis*, *A. binervia* and *C. littoralis*), as the canopy is actively replaced or augmented depending on whether it was destroyed by the fire or not.

It is clear from the data presented here that there can be no simple classification of plant responses to fires that adequately covers the potential range of post-fire behaviour (*cf.* Gill, 1981; Gill & Bradstock, 1992). Most of the species studied at 'Yarrowood' showed considerable spatial variability in their response to the low intensity fires, and several of the species may show considerably different responses when subjected to high-intensity fires. Furthermore, at least three of these species would fit into more than one of the categories defined by Gill (1981), as they have several recovery mechanisms. It is unlikely that any simple sub-division of these categories could be devised to incorporate variable responses, and it is therefore necessary to consider the type of fire being studied before species are assigned to particular categories (*cf.* Gill & Bradstock, 1992).

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